CONTRIBUTIONS TO THE ANATOMY OF MESOZOIC CONIFERS

NO. 2. CRETACEOUS LIGNITES FROM CLIFFWOOD, NEW JERSEY[1]

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(WITH PLATES XII–XV)

Araucarioxylon

One of the most interesting and, at the same time, most disputed questions in the phylogeny of the Coniferales deals with the relative antiquity of the abietineous and araucarian lines. The general ligneous structure of the latter has led the majority of botanists to its direct affiliation with the Cordaitales. In a recent paper, Professor JEFFREY[2] has shown that this resemblance exists only in the normal mature wood, and that in the seedling stem, root, cone axis, and traumatic tissue, there are present altogether different conditions. In these regions the rays often become thick-walled and heavily pitted, there are wood parenchyma cells, and the tracheary pits, instead of being closely approximated, are scattered and opposite. Moreover, in the cone axis the pits are separated by well marked cellulose bars of Sanio. All these features are characteristic of the Abietineae, and diametrically opposed to anything found in the Cordaitales. The locality of these digressions from the *Araucarioxylon* type is of especial significance. On both the zoological and botanical sides, the law of recapitulation is regarded as one of the fundamental conceptions of evolution, and according to this law it is in the plant seedling that ancestral features should be found. Further, case after case has been recorded where these primitive conditions are retained in the root and reproductive axis, and recalled in traumatic tissue. As

[1] Contributions from the Phanerogamic Laboratories of Harvard University, no. 63.

[2] JEFFREY, E. C., The history, comparative anatomy, and evolution of the *Araucarioxylon* type. Proc. Amer. Acad. 48:531–571. *pls.* 7. 1912.

instances of the first may be mentioned the occurrence of resin canals in the center of the root of such conifers as *Abies* and *Tsuga*, a harking back to the time when they were scattered throughout the wood, as in *Pinus;* as instances of the second, the presence of centripetal wood in the cone axis of *Equisetum;* and of the last, the ray tracheids in wounded specimens of *Abies*. It seems clear, therefore, from comparative anatomical and developmental evidence, that the Araucarineae are descended from ancestors which had thick-walled pitted rays, wood parenchyma, and scattered tracheary pits separated by bars of Sanio. These hypothetical ancestors are probably the Abietineae.

If such a conclusion is correct, we should expect to find fossil record of woods which possessed these modified araucarian structures, not only in primitive places, but also in their normal, mature growth. Recent investigation has shown such to be the case. For example, *Araucarioxylon Lindleyi* Seward, *Cormaraucarioxylon crasseradiatum* Lignier, and *Araucarioxylon noveboracense* Jeffrey have wood parenchyma; *Cormaraucarioxylon crasseradiatum* Lignier, *Protocedroxylon araucarioides* Gothan, and *Araucariopitys americana* Jeffrey have thick-walled pitted rays. Further, many of these Mesozoic araucarians have traumatic resin canals, as do *Abies*, *Cedrus*, etc. Up to the present, however, no fossil araucarian has been described with opposite pits or bars of Sanio. In an earlier paper[3] the writer has described several species of *Pityoxylon* from the Raritan Cretaceous of Cliffwood, New Jersey. These were included in a considerable amount of lignite collected by Professor JEFFREY, and turned over to the writer for investigation. In addition to the *Pityoxyla*, there were a number of *Cupressinoxyla*, and one *Araucarioxylon*. This last specimen was of especial interest in this connection, and will accordingly be described first.

The material consisted of a flattened stem about two inches in length and one in diameter. The preservation of the outer layer was but indifferent; near the center, however, it was excellent. The pith contains large masses of stone cells, similar to those of the living *Agathis*. Fig. 1 represents a radial section of the wood at

[3] HOLDEN, RUTH, Cretaceous *Pityoxyla* from Cliffwood, New Jersey. Proc. Amer. Acad. **48**:609–623. *pls. 4.* 1913.

some distance from the pith; fig. 2, the same at a higher magnification. The general araucarian nature of the specimen is vouched for by the thin rays, absence of wood parenchyma, and especially by the alternating and closely compressed tracheary pitting.

The structure next the pith is elucidated by fig. 4. At the extreme left are the ringed protoxylem and metaxylem elements, which, toward the right, are replaced by those of the secondary wood. In the first pitted tracheid the pits are uniseriate and scattered; in the second they are opposite. A careful examination of the wall between the pairs of opposite pits shows that they are separated by white lines. Fig. 5 represents these same elements at a higher magnification, and here the lines are still more conspicuous. The study of fossil *Pityoxyla*, a section of which is shown in fig. 8, has proved that the bars of Sanio in those woods are represented by similar white lines, a condition which would be expected from the cellulose nature of the bars, and the tendency of cellulose structures to disappear in the process of fossilization. That the white lines appearing in figs. 4 and 5 are also bars of Sanio seems unquestionable. The general resemblance of the pitting of this Cretaceous stem to that of the cone axis of *Araucaria Bidwillii* (fig. 7) is very striking. In the case of the latter, the cellulose composing the bars is still present, and stains a dark blue with hematoxylon, causing the bars to stand out as black lines in the photograph. In studying unstained living material, it would be possible to mistake the spirals of the primary wood for bars of Sanio. This possibility may be obviated, as JEFFREY has demonstrated, by using a double stain of hematoxylon and saffranin. The former stains the bars a deep blue and leaves the spirals untouched, while the latter stains the spirals a bright red. With fossil material, however, there is no chance for mistake. Here the protoxylem spirals, being lignified, persist, and appear as black lines (left of fig. 4); on the other hand, the bars of Sanio, being cellulose, drop out, and appear as white lines (right of fig. 4).

Fig. 3 represents a similar section from the same Cretaceous specimen. Toward the extreme left may be seen indistinctly a tracheid with metaxylem spirals; next it is one with approximately opposite pits. Near the lower limit bars of Sanio may be made out.

In the next tracheid the pitting becomes uniseriate again, and the bars of Sanio stand out with considerable clearness. Still a third case is presented in fig. 6. At the left are two spiral elements, and next them is a pitted element. Toward the upper end of the latter the pits are biseriate, with faint bars of Sanio; below they become triseriate, and then biseriate again. In the latter case they are alternate, but even here bars of Sanio are present. A similar combination of alternating pitting and bars of Sanio is shown in the tracheid at the right of fig. 7 (cone of *Araucaria Bidwillii*), and similar triseriate pitting in that at the extreme left.

This type of pitting is uniformly present in this specimen near the pith. Accordingly it seems to supply the only missing link in the chain of evidence pointing to the derivation of the Araucarineae from the Abietineae. All the araucarian features of wood structure have been previously shown to disappear in the primitive regions of extant araucarians, and now they have all been shown to disappear in the stem of extinct ones.

Brachyoxylon

Of the remainder of the Cliffwood lignites, a considerable amount belongs to the genus *Brachyoxylon*. In some cases twigs were found similar in almost every respect to such specimens as *Geinitzia Reichenbachi*, *Brachyphyllum macrocarpum*, etc., from the Cretaceous of Kreischerville, New York.[4] Figs. 9 and 10 represent transverse and longitudinal sections of one of these. The tracheids have the same combination of araucarian and abietineous pitting, the rays are smooth-walled, there is no wood parenchyma, and, furthermore, there are abundant sclerites in the pith. The particular specimen figured here is so like *Geinitzia Reichenbachi* in the shape and arrangement of stone cells that it seems safe to identify it with that species.

In other twigs, however, the arrangement of these sclerenchymatous elements is quite different. In figs. 11 and 14, for example, they are grouped to form nests, extending like plates, sometimes almost completely across the medulla. As shown in the photo-

[4] HOLLICK, ARTHUR, and JEFFREY, E. C., Studies of cretaceous coniferous remains from Kreischerville, New York. Mem. N.Y. Bot. Garden 3:1–38. *pls. 1–29.* 1909.

graphs, the individual cells are elongated longitudinally, and filled with a dark substance. This stem was one of the few with the bark still adhering. Figs. 12 and 13 show the details of the bast, and it is evident that, although in other respects it resembles closely some of the Kreischerville material, in this respect it is quite different. In *Brachyphyllum*, *Araucariopitys*, etc., the phloem is composed entirely of sieve tubes and parenchyma cells, while here there are tangential rows of bast fibers. This alternation of hard and soft bast commonly obtains in the Cupressineae (e.g., *Juniperus* and *Thuya*), Taxodineae (e.g., *Sequoia*), and Podocarpineae (e.g., *Podocarpus* and *Dacrydium*), and adds another to the points of resemblance between the araucarians and podocarps.

In addition to these twigs, there was a considerable amount of wood showing the same structure. Representative sections are shown in figs. 17–19. It seems to conform exactly to the *Brachyoxylon* type, both normally and traumatically. A number of pieces had been severely wounded, and in every case one or more tangential rows of resin canals extended from the wound cap; in one specimen there were as many as four concentric series. As shown in figs. 15 and 16, the canals are often small and constricted at intervals, like those formed traumatically in the Abietineae.

Cupressinoxylon

In addition to the *Pityoxylon*, *Araucarioxylon*, and *Brachyoxylon* described above, there are others belonging to the genus *Cupressinoxylon* Kraus. They have the same combination of araucarian and abietineous tracheary pitting without bars of Sanio, but differ in having wood parenchyma scattered throughout the year's growth. The most abundant of the stems of this type is represented in figs. 20–24. The pith is large and composed entirely of parenchyma cells (figs. 20, 21), without the sclerites characteristic of the *Brachyoxyla*. The wood is composed of tracheids, rays, and wood parenchyma. The tracheids are small, with uniserial pits on the radial wall. Usually the pits are scattered (fig. 23); rarely they are crowded, but in neither case is there the slightest indication of bars of Sanio. The parenchyma cells are relatively large, being sometimes three or four times the diameter of the tracheids. The rays

are low (figs. 23, 24), with thin unpitted walls. All the parenchyma, both radial and longitudinal, whether in pith, wood, or bark, is filled with a dense black substance. The structure of the phloem is shown in fig. 22. It consists of rays, sieve tubes, parenchyma cells, and also bast fibers. These last are usually more or less crushed, but it is not difficult to see that they occur in tangential rows, alternating with rows of soft bast, just as in the case of the *Brachyoxylon* twig described above. It is noteworthy that in the former specimen the soft bast collapsed and the hard retained its natural size, while here just the reverse is true. On account of the absence of bars of Sanio, such a wood as this, though strictly speaking a *Cupressinoxylon*, cannot be affiliated with other members of that genus, e.g., *Juniperus*, *Cupressus*, *Sequoia*, etc. On the contrary, its affiliations must be with the araucarians. The type genus *Paracedroxylon* was founded by SINNOTT[5] to include wood which is *Cedroxylon* in everything but bars of Sanio; and for similar *Cupressinoxyla* the genus *Paracupressinoxylon* was established.[6] Two species were described. The first, *Paracupressinoxylon cedroides*, resembles the Cliffwood specimen in question in absence of medullary stone cells, but differs in having thick-walled, heavily pitted rays like a *Cedroxylon*. The second, *P. cupressoides*, lacks pith and bark, but has exactly the wood structure of this Cretaceous twig from Cliffwood. It seems safe, accordingly, to include both specimens as *P. cupressoides*, in spite of the difference in horizon.

The stem just described, although the most abundant of the *Cupressinoxyla*, was the only one without stone cells in the pith. Figs. 25–28 represent a more common type. In the medulla may be seen groups of sclerites, and in the wood the scattered parenchyma cells. Fig. 27 shows the low rays and well spaced pits characteristic of the mature wood of this twig. Fig. 28 shows the structure near the pith. The pits here, instead of being distant, are fairly close, and are in several places separated by bars of Sanio.

[5] SINNOTT, EDMUND, A. W., *Paracedroxylon*, a new type of araucarian wood. Rhodora 11:165–173. *pls. 80, 81.* 1909.

[6] HOLDEN, RUTH, Jurassic coniferous woods from Yorkshire. Ann. Botany 27:533–545. *pls. 39, 40.* 1913.

Owing to the cellulose nature of these bars, they have dropped out in the course of fossilization, and now are represented by white lines. Their occurrence near the pith of this specimen, which is clearly transitional between the Araucarineae and Abietineae, is quite in keeping with their occurrence in the cone axis of the living genus *Araucaria*, and in the first annual ring of the fossil *Araucarioxylon* described earlier in this paper. In all these cases the bars of Sanio are to be interpreted as vestiges of what was characteristic of the mature wood of their ancestors, retained only in certain conservative regions of these reduced forms. Viewed in this light, it seems evident that their presence in the first formed wood of an araucarian *Cupressinoxylon* is another indication of the derivation of the Araucarineae from the Abietineae.

This stem is representative of a considerable number which differ from each other only in slight and unimportant details. The three diagnostic features are (1) wood parenchyma scattered throughout the year's growth, (2) thin-walled ray cells, and (3) scattered pits on the radial walls of the tracheids, without bars of Sanio intervening. All these are shown in figs. 27 and 29. In such structures as arrangement and size of medullary sclerites, there is considerable divergence. For example, in the specimen represented in figs. 25 and 26, the individual stone cells are grouped in small and irregular clusters, while in the case of the twig photographed for fig. 30 they form long lines extending down the pith. There is not a little variation also in the pitting of the radial walls of the rays, though in all the horizontal and end walls are unpitted. Usually there are one to four small piceform pits to each crossfield, but in fig. 31 is shown a specimen with a single large pit. That each large pit originates from the fusion of two small pits is indicated by the occurrence of two partially fused pits, end to end. Similar stages in pit fusion were described in the case of one of the *Pityoxyla* from the same deposit. Another interesting feature of this specimen, shown in fig. 32, is the resinous exudation from the rays into the tracheids. Similar appearances are common in the living *Agathis*, and thus serve to establish another bond between these transitional Mesozoic forms and living members of the Araucarineae.

Summary

1. An *Araucarioxylon* from the Raritan Cretaceous of Cliffwood, New Jersey, shows bars of Sanio near the pith of the stem, similar to those on the cone axis of the living Araucarineae.

2. *Brachyoxyla* from the same locality are as a rule very similar to those from Kreischerville, Staten Island, differing only in such details as arrangement of medullary sclerites and structure of the bast.

3. The *Cupressinoxyla* of Cliffwood all lack cellulose bars of Sanio in the mature wood, and should on that account be placed in the new genus *Paracupressinoxylon.*

4. The occurrence of three absolutely typical *Pityoxyla*, and not a single typical *Araucarioxylon*, among these lignites seems to indicate that in tracing back the families of living conifers it is the Abietineae which remain unchanged, and the Araucarineae which become less and less like living representatives of that family. The same conclusion may be drawn from a consideration of the lignites of Staten Island.

5. The variety of structure of these Mesozoic araucarians has its bearing on the question of the monophyletic or diphyletic origin of the Coniferales. There are certain features which have been supposed to sharply differentiate the araucarians from the other families. Both fossil and comparative anatomical evidence demonstrate the fallacy of this view. As regards wood structure, every feature of the Abietineae—resin canals, bars of Sanio, thick-walled pitted rays, wood parenchyma (terminal and diffuse), even to as small and unimportant details as fusion pits in the rays and regularly alternating bands of hard and soft bast—has been found in the Araucarineae, living or extinct. As regards strobilar anatomy, EAMES[7] has shown that the stages in the reduction of the female cone are closely paralleled in various cupressineous and taxodineous genera, and the writer[8] has shown that in one Mesozoic araucarian (*Voltzia*) there was a double cone scale, like that of the living genus

[7] EAMES, ARTHUR J., The morphology of *Agathis australis*. Ann. Botany 27:1–38. *pls. 1–4.* 1913.

[8] HOLDEN, RUTH, Some fossil plants from eastern Canada. Ann. Botany 27:243–255. *pls. 22, 23.* 1913.

Cryptomeria. In view of all the facts, it seems evident that the conifers, as a whole, are derived from the same ancestral stock, and that the Abietineae are more like that stock than the Araucarineae.

This investigation was carried on in the Phanerogamic Laboratories of Harvard University, and the sincerest thanks of the writer are due to Professor E. C. JEFFREY for the lignites from Cliffwood, for the photograph of the cone of *Araucaria Bidwillii* (fig. 7), and for many helpful suggestions in the course of the work.

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EXPLANATION OF PLATES XII–XV

FIG. 1.—*Araucarioxylon* sp.; radial section of mature wood; ×125.

FIG. 2.—Same, showing alternating and crowded pits; ×250.

FIG. 3.—Same, near the pith; toward the left, a tracheid with opposite pits and bars of Sanio; toward the right, one with uniserial pits and bars; ×500.

FIG. 4.—Same; at the left are the primary wood elements; next, a tracheid with scattered pits; and then one with opposite pits and bars of Sanio; ×250.

FIG. 5.—Same, more highly magnified; ×500.

FIG. 6.—Same, showing opposite, triseriate, and alternating pits, in every case separated by bars of Sanio; ×500.

FIG. 7.—*Araucaria Bidwillii;* radial section of cone axis in proximity to the protoxylem, showing presence of bars of Sanio; ×500.

FIG. 8.—*Pinus protoscleropitys;* radial section of mature wood showing opposite pits and bars of Sanio; ×500.

FIG. 9.—*Geinitzia Reichenbachi;* transverse section of stem, showing sclerites in pith; ×15.

FIG. 10.—Same; longitudinal section of pith; ×15.

FIG. 11.—Twig from Cliffwood; transverse section of pith, including nest of stone cells; ×15.

FIG. 12.—Same; the outer bark contains clusters of large stone cells, below which is the inner bark, consisting of alternate layers of hard and soft bast; ×40.

FIG. 13.—Same; longitudinal section of bark; ×40.

FIG. 14.—Same; longitudinal section of pith, showing nests of stone cells; ×15.

FIG. 15.—*Brachyoxylon* sp. including row of traumatic resin canals; ×40.

FIG. 16.—Same; longitudinal section; ×40.

FIG. 17.—*Brachyoxylon* sp.; transverse section of normal mature wood; ×90.

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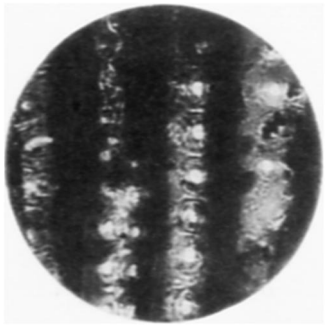

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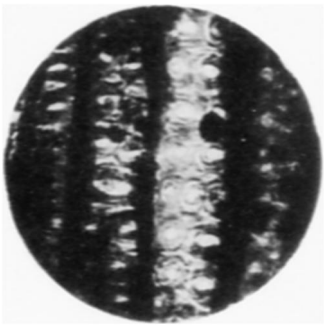

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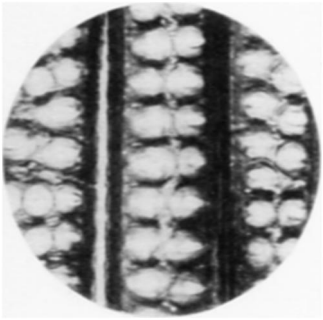

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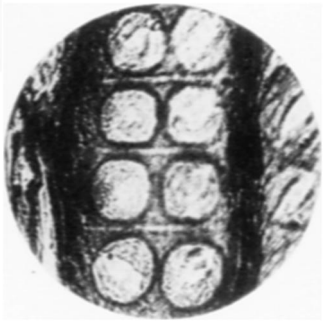

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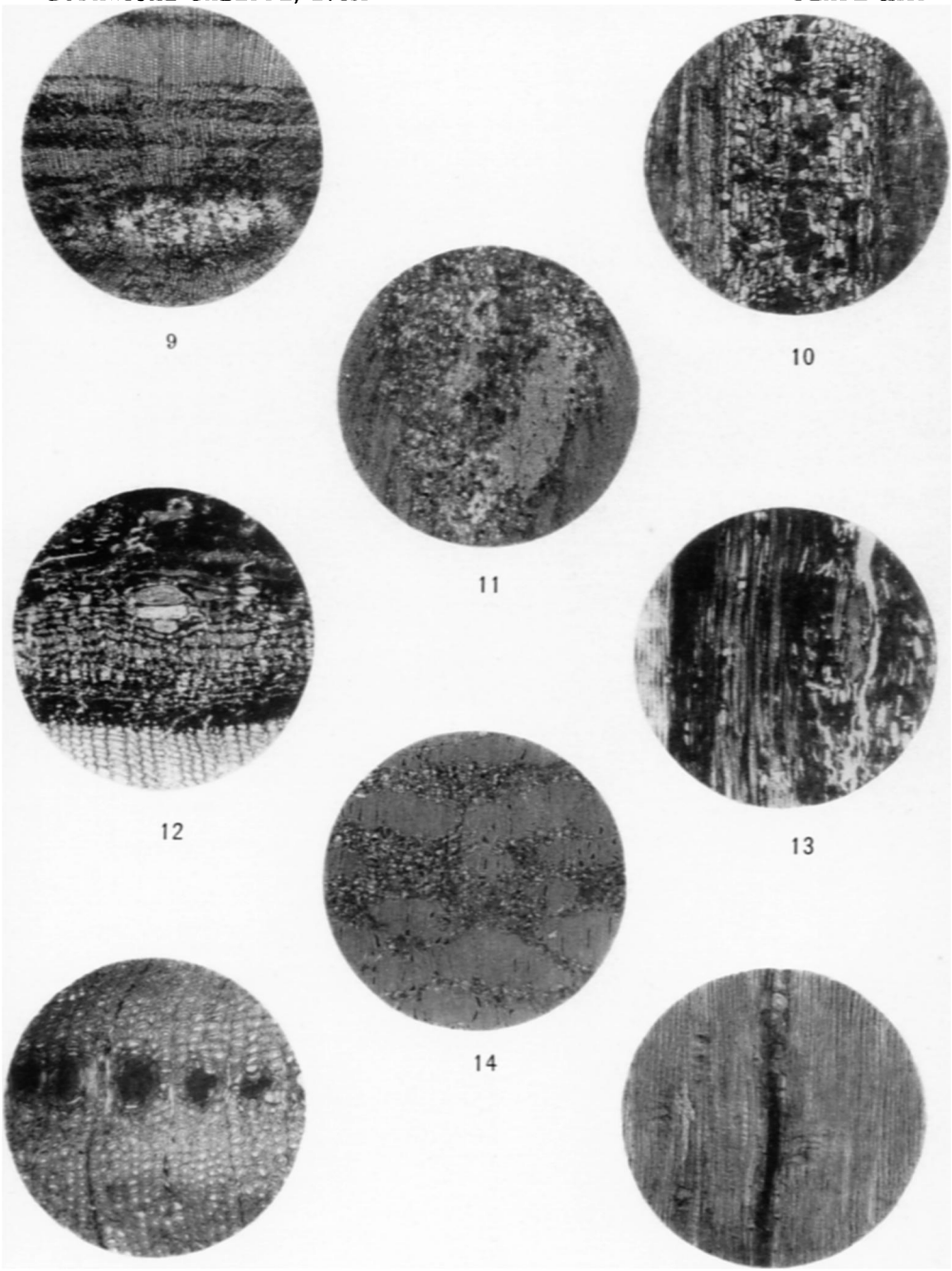
HOLDEN on CRETACEOUS LIGNITES



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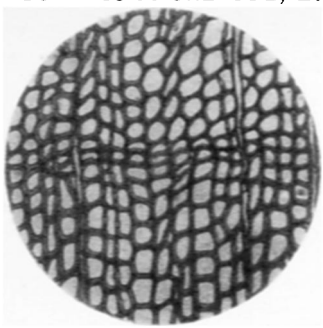

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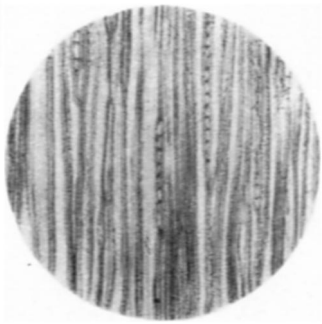

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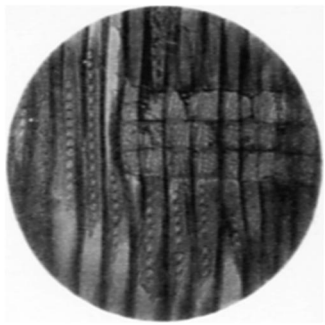

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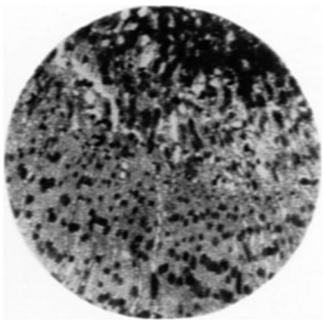

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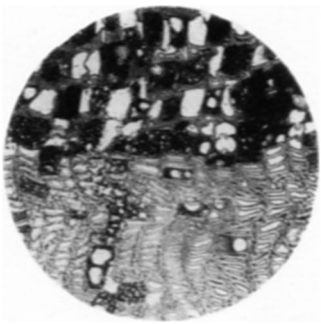

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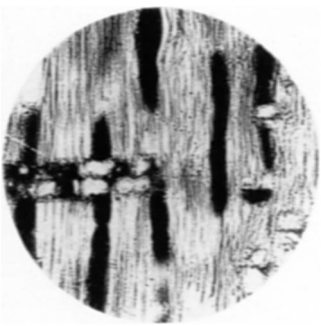

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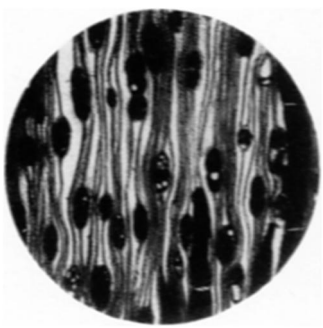

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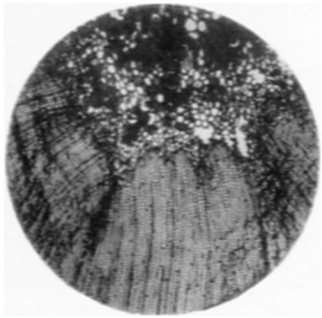
HOLDEN on CRETACEOUS LIGNITES



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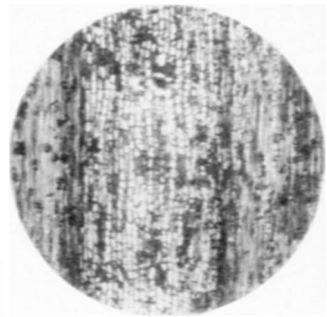

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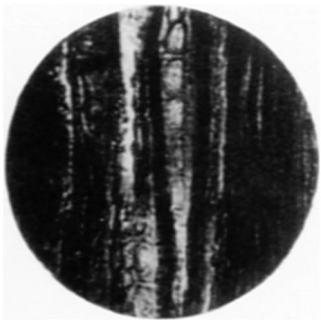

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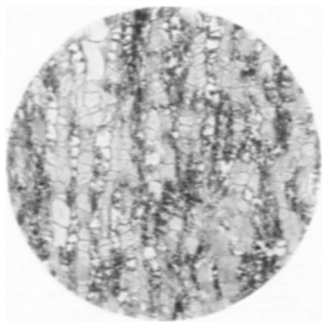

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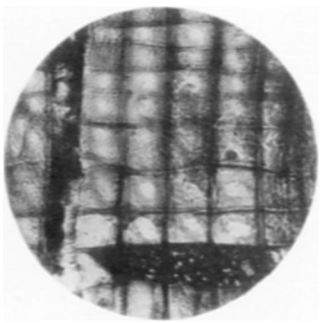

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HOLDEN on CRETACEOUS LIGNITES

FIG. 18.—Same; radial section, showing tracheary pits sometimes crowded and sometimes scattered; thin-walled rays, with numerous small pits on longitudinal wall; ×90.

FIG. 19.—Same; tangential section, showing tangential pitting; ×90.

FIG. 20.—*Paracupressinoxylon cupressoides;* transverse section near pith, showing abundance of parenchyma cells; ×15.

FIG. 21.—Same; longitudinal section; ×15.

FIG. 22.—Same; transverse section including bark and wood; in the former the large parenchyma cells and crushed fibers may be seen; ×90.

FIG. 23.—Same; radial section, showing low, resinous rays, large parenchyma cells, and scattered tracheary pits; ×90.

FIG. 24.—Same; tangential section; ×90.

FIG. 25.—*Paracupressinoxylon* sp.; transverse section, showing stone cells in the pith, and wood parenchyma; ×15.

FIG. 26.—Same; longitudinal section; ×15.

FIG. 27.—Same; radial section of mature wood; ×40.

FIG. 28.—Same; section near pith, showing bars of Sanio; ×250.

FIG. 29.—Another specimen of *Paracupressinoxylon* showing wood parenchyma, scattered tracheary pits, and thin-walled rays; ×90.

FIG. 30.—Another specimen, showing peculiar arrangement on stone cells; ×40.

FIG. 31.—Another specimen, radial section, showing fusion pits in the rays; ×150.

FIG. 32.—Same; tangential section, indicating resinous exudations in tracheids from rays; ×90.